The food of *Collocalia* swiftlets (Aves, Apodidae) at Niah Great Cave in Borneo[1]

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(*With a plate*)

I. BORNEO CAVE SWIFTLETS IN THE REGIONAL CONTEXT

The Great Cave at Niah (113°48′E, 3°47′N) lies 13 miles behind the South China Sea near Miri in northern Sarawak, a state in Malaysian Borneo. It soars to 220 feet high, 800 feet wide at the largest (west)

[1] Received November 1972.

of five main mouths, the bottom of which is still above the forest canopy below. The 27-acre floor has yielded some of the oldest pre-historic human remains yet for the area (Harrisson 1964a; Ripley 1967 : 168-72 ; Howells 1972 : 13). The geologically not very old Niah (Subis) limestone (Wilford 1964) is honeycombed with chimneys, tunnels, grottos. In this vast labyrinth, a sort of huge gruyère cheese, throughout the equatorial year move and roost some 4,500,000 swiftlets (Apodidae) of three species, though the third and very much less numerous *Collocalia esculenta* only frequents the light sections. Intimately intertwined with the birds are at least half a million bats of seven resident species, six insectivorous (Medway 1958b ; Harrisson 1967). This teeming mass feeds through and/or *over* the permanently green rainforest which inland runs almost unbroken into the sparsely inhabited interior (Harrisson 1959a; Richards 1936).

At dawn (soon after 0600 hours Malaysian Local Time = 2330 GMT) the great part of this bird population pours out, to remain away twelve or more hours on the wing, while dense streams of bats come back the other way. Before dusk (sunset *c.* 1830 LT) the process is reversed. This terrific traffic would be unmanageable were it not that all but one of the bats and both the dark-roosting birds give out constant echo-location signals. *Collocalia* is one of only two bird genera—the other *Steatornis* of central American caves—with this specialization (Griffin 1958 ; Medway 1959 ; Harrisson 1964b). Although this system possibly is *not* sufficiently refined to enable insect-catching in the dark, it can be valuable in extending dusk for late insect swarms and on moonlight nights (cf. Medway 1962 ; T.H.).

The writer began the Sarawak Museum's investigations at Niah in 1954 and has since spent eleven 'seasons' totalling three years, largely living inside the caves (Harrisson 1957 ; 1959b ; 1970). In 1957 we recruited Loid Medway to develop the faunistic side of the project, with rewarding results now well-known (Medway 1958a, etc ; Harrisson & Medway 1962, etc.). The present study is firmly based on that earlier shared experience, plus the felt need to supplement one somewhat neglected aspect of the previous major swiftlet study (Medway 1962, cf. 1968) : the food problem. Indeed, mainly because of the difficulty of identifying tiny insect fragments from out of these delicate little birds and the impossibility of detecting what they take closely on the wing, swiftlet food has everywhere tended to be taken for granted. Even in the second edition of his great THE BIRDS OF BORNEO, B. E. Smythies (1968 : 292-7) conspicuously omits the FOOD section for *Collocalia* species.

Hitherto most of the meagre information for the Oriental Region (as defined by Sálim Ali 1964) has come from the Indian sub-region. This is summarized in Sálim Ali & Dillon Ripley's HANDBOOK (1970, **4**: 27-32), which files a nil report for food of *C. maxima*, there well-named the Black-nest Swiftlet (in Malaysia previously, unsuitably, Low's Swiftlet; cf. Medway 1966; Smythies 1968). Sálim Ali & Ripley suggest it is 'doubtless' as their No. 683, the closely similar *C. brevirostris*, the Himalayan Swiftlet, said to take 'mainly dipterous and hymenopterous insects'. More exact information is given for the closely related Indian Edible-nest Swiftlet, *C. unicolor*. Four stomachs, studied in February, held two forms of mango-hopper (also at Niah, III, ii, below), other Hemiptera-Homoptera, Coleoptera, Odonata, Hymenoptera, Diptera and Trichoptera ; no emphasis on ants, no mention of termites (Isoptera).

At Niah we have the interesting situation where two monocolour species co-exist: *C. maxima lowi*, with the 'Black-nest' (edible when cleaned), and *C. salangana natunae*, the Mossy or Thunberg's Swiftlet (cf. Medway 1961), the former more numerous but both mixed up, nesting inside one cave. They are almost indistinguishable in flight, sometimes difficult even in hand. The only fairly sure differences are over 129 mm wing and more feathered tarsus for *maxima* ; wing 119-129 mm, and little or no tarsus feathering on *salangana*. Each species normally nests once a year on numerous but separate patches of wall ; *maxima* lays one egg, *salangana* two. Both have protracted breeding cycles, minimum 5 months and up to 7 for *maxima*, peaking broadly between November and March.

From 1947 I was responsible for controlling and conserving swiftlets in this and other caves, including 'harvesting' edible *maxima* nests. Despite extensive exploitation, the Niah population has not decreased—as will be seen in what follows, it may well be near saturation (cf. Medway 1957 ; Gibb & Harrisson 1959 ; Harrisson 1964b).

II. Aerial flight and feeding observations

(i) *Super-canopy : lateral scatter*

First, where do Niah's millions feed ? Although all Borneo observers have agreed that the dark-nesting swiftlets only casually feed over clearings and inhabited areas, never *under* tree-cover, little more was known. This observer spent nearly 350 hours during 1962-72, mainly in helicopters, establishing an absolute dominance of swifts (5 species) and especially swiftlets (3) as regular super-canopy operators. No other birds except a few Hemiprocnidae were normally feeding at this level, though some eagles hunt downward *into* the forest. Nineteen others were seen in local or migratory flight, only hornbills regularly.

TABLE 1

BIRDS SEEN ABOVE THE BORNEO FOREST CANOPY

(compiled from Harrisson 1963 ; 1966 ; and 1972 unpublished)

Family		No. of species identified	No. of separate sighting incidents	Incidents 1000 ft.+ above canopy	Remarks
Ciconiidae	Storks	1	2	0	
Accipitridae	Hawks & Eagles	13	56	11	Mostly *Spilornis* 2500′
Columbidae	Pigeons	3	13	0	
Apodidae	(*a*) *Collocalia* spp.	3*	2200+	*c*. 50	?*maxima* occ. over 2000′
	(*b*) other true swifts	1	14	2	*Chaetura gigantea*
Hemiprocnidae	Tree Swifts	1†	12	0	—
Coraciidae	Rollers	1	7	0	—
Bucerotidae	Hornbills	6	*c*. 260	1	*Aceros undulatus*
Picidae	Woodpeckers	1	1	0	—
Passerines	(all families)	7	10	1	*Gracula religiosa*
	Total	37	2200+375	50+15	

* *C. salangana* and *maxima* plus *C. vestita* in the Baram basin—not at Niah (Smythies 1968).

† *H. longipennis*, which *mainly* feeds over secondary jungle and clearings.

Lateral spread of super-canopy swiftlets proved erratic. Probable Niah birds were seen far inland, but there is no way of being certain of source at any distance. Sustained helicopter sorties to clarify this aspect in the vicinity of the caves and over the coastal plain during August-December were not fully successful. Co-ordinated with ground watch along the river and one road line (since 1965) on some days, especially if fine, at *any* season, the great mass of birds is not visible within 10-25 miles of the limestone massif. On 20-21 December, as an extreme example, 4 hours' intensive flying mostly north and west of Niah produced only one swiftlet ; simultaneous ground records showed the cave nearly empty of birds at the same times (II, iv, below).

Medway (1962 : 229) had ' never seen *maxima* or *salangana* more than 15 miles from the cave '. But there was then no good way to observe beyond that distance and limited facilities for seeing over the canopy anywhere. On that basis, his own figure (same sentence) of ' at least four million resident adults ' would mean a super-canopy all-day density of 6,000 birds per square mile, even ignoring that the immediate radial land is heavily deforested or cultivated (rice, pepper) and thus only suitable for *C. esculenta* foraging.

Both *salangana* and *maxima* have been timed flying at 25-30 m.p.h. Most are usually away at least 11 hours a day. 50-75 miles inland will take them over huge tracts of virgin jungle, still incompletely explored on the ground (Harrisson 1959a ; Richards 1936), widely without other limestone to support ' competing ' cave populations (cf. maps in Wilford 1964 ; list in Smythies 1968 : 71). Otherwise, surely, the vast Niah insectivorous population—birds and bats—might be insupportable through the year, including long wet periods which flood the forest floor in the immediate vicinity ?

(ii) *Vertical trends*

About 2% of swiftlets were seen 1000 ft or more above the canopy (Table 1)—birds crowding and spiralling immediately over the cave gorge to come in the dusk inrush are not feeding (Medway 1962 : 231 agrees). The large majority move between 20 and 800 feet, without recognizable stratification (Harrisson 1963). There may be a tendency for *maxima* to feed higher at times, but no distinct or regular trends could be found—certainly not to the extent postulated quite theoretically by Medway (1962 : 243), who put *salangana* at ' intermediate ' levels and *maxima* higher.* Except directly over limestone, any swiftlet (and perhaps any insect ?) above 1500 feet super-canopy is quite a rarity (Harrisson 1966 : 419).

In March 1967, with *maxima* nesting strongly, a special effort was made to search higher air levels in case birds had previously been missed. None were located.

The evidence so far in this difficult aerial field indicates *maxima* only erratically flying high but tending to go further afield and stay out longer when ' necessary ' (see below).

(iii) ' *Swarming* '

Collocalia concentrations of *c.* 50 to *c.* 500 were seen associated with dense swarms of unidentified flying insects, again very erratically. Swarming ants and termites may be periodically crucial in the food supply (III below). Unfortunately, almost nothing is known on controlling factors in the region (see Appendix).

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* In the summary of his long paper, Medway (1962 : 245) restates his earlier hypothesis as if it was proven (' *C. maxima* feeds higher than *C. salangana* '). Interestingly, the larger *C. gigas* of Java ' tends to feed higher ' than other *Collocalia*, according to Becking (1971). But elaborating, this experienced observer makes clear his observation was largely over *open* country, and that *gigas* came low also ' in particular when there are flying termites ' (Becking 1972). All but one of the few *gigas* records for Borneo are low-flying in the open (Smythies 1968). There is no present evidence that ants or termites swarm tropically *high*, rather the contrary (Nutting 1969; Deligne 1972).

(iv) *Movements through the cave formation*

The broad flow patterns into and inside the limestone have been very adequately described by Medway (1962). Further study, incorporating mist-nets (since 1964), requires only three new emphases (T.H.):

(1) More swiftlets, especially *maxima*, stay out part of the night than was earlier recognized, especially with clear moonlight.

(2) Both fly at all levels inside, according to internal topography, though the proportion of *salangana* tends larger lower down towards the floor.

(3) Although rain and storms visible from the caves immediately inhibit *Collocalia* movements in the vicinity, on a wider view they can, like other swifts, operate around considerable storm patterns (cf. Lack 1958). This can be a factor delaying evening return, too (and cf. Nutting 1969).

III. Laboratory analyses

(i) *Stomach contents*

Many swiftlets netted on the dusk inrush have the stomach so distended that it bulges conspicuously through the belly skin. But returning-to-rest birds are equally often almost empty, including at peak nesting (March-April).

Contents of a full *salangana* stomach weigh near $1\frac{1}{2}$ grams, *maxima* $1\frac{1}{2}$ to 2 grams, averaging near 11% body weight. 100 full stomachs examined on the spot had 27 to 232 individual insects (cf. Table 7) most of those over 100 in *salangana*. Numbers depend primarily on proportions of tiny beetles and flies (2-4 mm) rather than larger types of termite (13 mm) and ants (see Table 11).

We can estimate that the year round Niah Swiftlets *eating well* could daily use *c.* 5000 kilos; involving not less than 100,000,000 individual insects each 24 hours?

Nestling stomachs (65) show the same varying food types as adults in other seasons (Tables 2-5). A 21-day *maxima* was distended with 26 whole ants, 6 large termites and beetles (11+ species); at the other extreme, a 3-day chick had only tiny hard beetle fragments. Fledgelings under favourable conditions can survive without food for 15+ days, an important ability under these conditions (see below).

(ii) *The food spectrum*

In addition to on-the-spot stomach examinations (as above), 41 were preserved for fuller laboratory study. This was undertaken with the most generous help and expertise of Dr G. H. L. Rothschild (1965-8), research entomologist in the Department of Agriculture, Sarawak ; and later extended at Cornell University, N.Y., with the generous and patient help of Dr W. L. Brown Jr. (1968-71), Professor of Entomology there and Hon. Curator of the important Harvard University collection of ants, on specimens which could not be adequately identified earlier in Borneo. The results incidentally give the first information on what, other than birds, moves over the Borneo canopy.

The main material was 23 *maxima* and 18 *salangana* netted in dusk samples, November and March (breeding peak) at Niah, with a separate February check sample from the Kakus caves, 100 miles to the southwest (10 *maxima*, 3 *salangana*). In view of the many lacunae in area entomological knowledge, identifications were aimed at main groupings only.

Over half the food materials were Hymenopteran ; at times this reached 99% for *maxima* (Table 4).

TABLE 2

THE ORDER HYMENOPTERA IN *Collocalia* STOMACHS

Family		Subfamily	*C. salangana*	*C. maxima*	Minimum no. of species involved
Formicidae	Ants	Camponotinae	very common	v. common	6
		Myrmicinae	abundant	abundant	15
		Ponerinae	occasional	fairly regular in small nos.	4
Ichneumonidae	Parasitic wasps		fairly regular	none	3
Chalcidoidae	Parasitic wasps		occasional	none	2
Meliponidae	Stingless bees [*Trigona*]		*once	once	1
					31

Five other insect orders are present, with 34 species ; though in actual frequency the alate of one large Macrotermitinae species dominates this sector (Table 7, etc.).

* See Appendix.

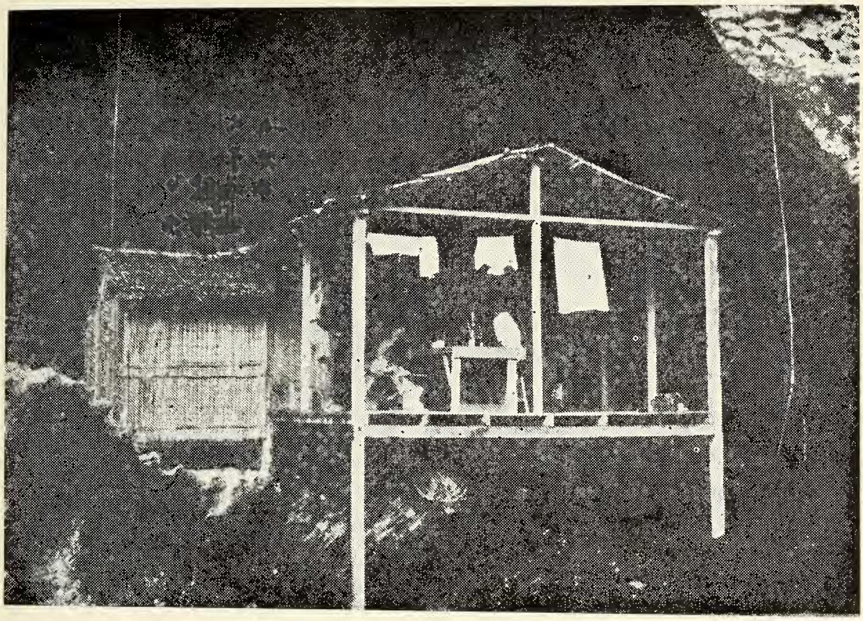

Fig. 1. Field laboratory for cave studies, Niah Great Cave, Sarawak.
(*Photo*: *Barbara Harrisson*)

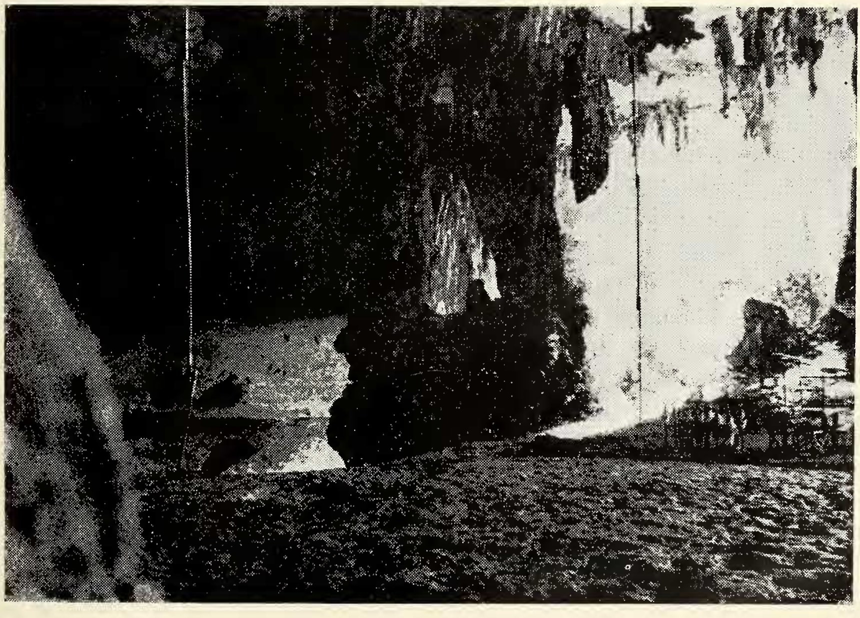

Fig. 2. Part of west mouth of Niah Great Cave, showing mist-netting area near big central stalactite and two birds-nester's climbing poles (up to 200 ft high).
(*Photo*: *Christine Harrisson*)

TABLE 3

OTHER INSECTS IN *Collocalia* STOMACHS

Order	Family		*C. salangana*	*C. maxima*	Minimum no. of species involved
Coleoptera	Platypodidae		common	once	3+
	Histeridae		once	none	1
	Scolytidae	Woodborers	common	occasional	3
	Elateridae	Click-beetles	regular in small nos.	once	4+
	Brenthidae		once	none	1
	'Other beetles'		occasional	fairly regular	2+
					14
Hemiptera	Lygaeidae	Plant bugs	fairly reg.	fairly reg.	4
Homoptera	Cicadellidae	Leaf-hoppers	occasional	none	2
	Delphacidae	Plant-hoppers	once	none	1
					7
Diptera	Culicidae	Mosquitoes	fairly reg.	occasional	4
	'Other Nematocerid flies'		occasional	once	1
	Stratiomyidae		occasional	once	1+
	Lauxaniidae		once	none	1
	Cylindrotomidae		once	none	1
	'Other Brachyceran flies'		occasional	occasional	2+
					10
Isoptera	Termitidae (Macrotermitinae)		abundant	very common	3
				Grand Total:	34

Since we do not know anything about invertebrate life super-canopy, it is not possible to assess how far these two lists, covering 65 species of 5 orders, reflect a cross-section of available flying food. The absence of a single Orthopteran may be noteworthy, though these are mostly large (over 15 mm) in Borneo. Light-winged Trichoptera and Odonata (dragonflies) are also possible absentees. Softness or hardness alone are not final selective factors, since both swiftlets tackle the hardest-headed Carpenter Ants (e.g. *Colobopsis*) as well as tiny mosquitoes; these have been identified in nestlings, too.

(iii) *Ants in particular*

One occasionally finds adult *salangana* without ants (e.g. one with 21 termites and 51 other insects, Nov.) and *maxima* often without termites and with only a few ants (min. 5). But ants remain constantly the commonest feed, though sometimes flooded out by larger, fatter termites. Dr Rothschild calculated the gross stomach contents for the two Niah samples:

TABLE 4

PERCENTAGE OF FOODS IN *Collocalia* STOMACHS (& cf. Table 6)

Food	Novmber		March		'Average'
	C. salangana	*C. maxima*	*C. salangana*	*C. maxima*	both species
Ants ..	57%	46%	37%	99%	60%
Termites ..	33	43	32	0	27
Other ..	10	11	31	1	13

Termites are of three unidentified 'types' (i.e. at least 3 species ?), all Macrotermitinae. Type 1, fattest and largest (13 mm) comprises two-thirds of such food ; type 2, fat but small (3·5 mm) forms about one-third ; type 3, tiny (2 mm), only 1%. Type 1 frequently occurs alone ; 2 and 3 usually mixed with 1.

By contrast, we have at least 25 species of ants identified to genus or beyond. In Professor Brown's view the forms represented are those from the whole range of ants one might reasonably expect to find in Borneo. His subsequent examination confirmed Dr Rothschild's earlier (1968) view that 'the two echo-locating swiftlets of Niah consume the whole taxonomic spectrum of flying ants, without any *entomologically* discernible specialization or exclusion'.

From 19 stomachs the sex for 40 ants of 12 genera was determined. A heavy female preponderance, 35 : 5, is consistent with their generally much fatter swarming condition (see Appendix). Significantly, in no case were both sexes of the same genus found.*

Sexed ants were : 5 MALES—*Paratrechina* (2), *Rhopalomastix* (2), *Amblypone* (1) ; 35 FEMALES—*Camponotus* (11), *Crematogaster* (5), *Cladomyrma* (5), *Pseudolasius* (4), *Petramorium* (3), *Hyponera* (3), *Brachyponera*, *Trachymesopus*, *Pheidologeton*, and 'a small myrmicine'.

* Every identified ant of all three subfamilies was found at least once, usually several times, in both *salangana* and *maxima*.

Other, unsexed, genera include *Colobopsis*, *Polyrachis* and *Solenopsis* (all common), probably *Emeryopone* and several unnamed myrmicine genera.

The following were identified down to species :

Trachymesopus darwini—the very common ' flying ant ' at lights in settlements in Borneo ; not common in cave food.

Tetramorium guineense—a world-wide ' tramp ', originating in Africa ; *mainly* terrestrial ; twice in food.

Camponotus of *cottesi* and *impressus* groups—big-headed Carpenter Ants ; very common in this food, including over a third of all the March *maxima* samples (sparsely in *salangana* then).

Brachyponera jerdoni—occasionally, singly, in food.

38 stomachs provided satisfactory material to check the number of ant genera present, a point relevant to the number of swarms foraged in any one food-sequence.

TABLE 5

NOS. OF ANT GENERA IN 38 *Collocalia* STOMACHS

No. of genera identified		% of all birds (both species) in this number	
One only	..	26%	63%
Two	..	37	
Three	..	18	
Four or Five	..	12	
Six or more	..	7	

Out of the quarter taking simply one ant-form 4, all *maxima*, had *nothing* else to eat. The rest had supplementary termites or other insects. Moreover, no one adult had more than 16 of any one ant-form. Notable in comparison was a well-grown *maxima* nestling (19 November) with ants of at least 9 species, along with 5 large termites, a whole borer-beetle and 2 fragmented flies.

(iv) *The total meal*

To see the food pattern more closely (cf. Table 4) let us next glance at a single sample of 13 adults caught in one mist-net within dusk-rush minutes, 29 March. Both species then had young in nest ; and *maxima* nest-harvesting was over. (A minority, this day estimated under 5%, had come in before inrush.)

TABLE 6

13 *Collocalia* STOMACHS IN SINGLE INRUSH NET (29 MARCH)

Species	Sex	No.	No. of Ants smaller mostly	No. of Ants larger mostly	No. of Termites Type 1	No. of Termites Types 2-3	No. of Other Insects	Total all
salangana	♂	4	181	1	79	34	196	491
	♀	4	81	2	94	48	25	250
		8	262	3	173	82	221	741
maxima	♂	3	14	147	0	0	0	161
	♀	2	18	4	0	0	1	23
		5	32	151	0	0	1	184

On this flash-sample, there is a clear-cut distinction: *salangana* on termites, smaller ants and other insects; *maxima* on larger ants. But individual variation is high. Indeed 1 ♀ *salangana* had zero termites and accounts for 127 of the 'other insects', while ♂ and ♀ *maxima* had only smaller ants. Species and sex differences are immediately diluted by comparison with another sample. For instance, if we switch a month earlier and 100 miles to the Kakus caves, further inland, with smaller numbers of both species living together in the same way, the apparent *salangana* dependence on termites vanishes. Neither swiftlet has taken one. Or going back to November at Niah, some of both *maxima* and *salangana* were then distended on termites, others had none, though as in March the smaller bird had considerably more termites, especially the largest (Type 1).

TABLE 7

AVERAGE OF 3 INSECT GROUPS PER STOMACH, 3 PERIODS

Month	Species	No. in sample	Average no. of individuals per stomach of Ants	Average no. of individuals per stomach of Termites	Average no. of individuals per stomach of 'Other'	All three
November	*salangana*	7	25	14	5	44
	maxima	9	7	5	1	13
February	*salangana*	3	22	0	6	28
	maxima	9	11	0	1	12
March	*salangana*	8	33	32	28	93
	maxima	5	37	0	0	37

On each occasion *salangana* had more than twice as many items per bird as *maxima* (cf. III, vi). The total termitelessness of March *maxima* (Table 7) was repeated for both in February, but neither in November. The process can be clarified another way :

TABLE 8

NOS. OF *Collocalia* STOMACHS WITHOUT A SINGLE EXAMPLE FOR 3 GROUPS (3 PERIODS COMBINED)

Species	No. of birds	Individual stomachs without one :		
		Ant	Termite	'Other'
C. salangana	18	2	8	5
C. maxima	23	2	21	15

This well brings out the relative frequency of termitelessness, and the correlated but lesser neglect of any insect other than ants. One of the two termite-eating *maxima* above had *only* termites, 36, entire. Several *maxima* nestlings and adults earlier examined at the caves had whole large termites too.

(v) *Swallowing and fragmentation*

Swiftlets swallow whole insects of all sorts. There are, however, notably often fewer termite wings than bodies in stomachs (see vi). Some smaller items, especially Diptera, rather surprisingly remain intact—even with wings after transfer from adult food 'pellet' to nestling stomach. For others, especially beetles, both whole ones and separate hard elytra occur, as with two March *salangana*.

TABLE 9

BEETLE (ONLY) REMAINS IN TWO *salangana* STOMACHS

Family	Length	Bird no. 1	Bird no. 2
Platypodidae ..	3·5	50 whole + 78 elytra	12 whole + 26 elytra
Scolytidae ..	2·5	12 whole + 25 elytra	13 whole + 26 elytra

This suggests long survival of some hard parts which may well serve a secondary function, remaining in a slower digestive cycle than is presently understood and perhaps peculiar to *Collocalia*—which already has nest salivation and echo-location as precedent specialisms for success in this remarkable cave-niche.

(vi) *Size factors*

From complete or re-assembled specimens we were able to calculate the original body size of nearly all the food insects. This further labour seemed essential in view of the above somewhat negative conclusions on species-differentiation by other criteria, as well as to test a second suggestion (cf. II, ii) by Medway to explain the Niah *Collocalia* situation. Following general western theory (cf. Lack 1947) he concluded (1962 : 240) that as 'the two species must have different ecology' so, where feeding overlaps aerially, they each 'select different elements from the airborne prey' according to bill size. This was re-examined at Niah in 1965. Consistent with longer wing and higher body weight, *maxima* gape there averages *c.* 1 mm more than *salangana.* Does this directly affect size intake ?

In the case of the 'other' insect group, the problem hardly arises, since over 95% of these are *c.* 5 mm or less.

TABLE 10

APPROXIMATE BODY LENGTH OF VARIOUS 'OTHER' INSECTS TAKEN REGULARLY BY *Collocalia*

Order	Family	Average length (mm)	Maximum length (mm)
Hymenoptera	All wasps, bees	2·0-3·5	5·0
Hemiptera	All sorts	3·5-5·0	5·5
Coleoptera	Scolytidae	2·0	2·5
	Platypodidae	2·0-3·0	3·5
	Elateridae	3·0-4·0	5·0
Diptera	All sorts	2·5-3·0	3·0

At this size level, clearly no size differentiation by bird species can be detected ; indeed the slightly larger wasps and bugs are, on these data, less likely to be taken by the larger bird (cf. Tables 2 and 3). It is fairly safe to suspect both swiftlets may take pretty well anything of this size they come across, and that the absence here of a few small items for *maxima*—only one of which occurs at all regularly with *salangana* (Table 2)—is partly chance on small series, though partly, also, a reflection of a less *positively* 'omnivorous' approach and relatively less consumption of beetles and flies perhaps.

The earlier noted absence of certain other possible super-canopy forms, such as tiny dragonflies, need not be truly selective, but for the less obvious reason that with such insects in flight *stiffness* or angle of wing, rather than actual span, may restrict the capacity to swallow. Although larger winged termites and some large flying ants are taken at more than twice the sizes of Table 10, the wings of many of these fall off or fold inward on touch (Nutting 1969 : 258 ; T.H.). It is extremely difficult to differentiate all such wings in stomach analysis. Certainly, of 255 measured termites taken, 67% were over 12 mm long ; present in both swiftlets but mainly *salangana* (Tables 6-8).*

The 25 ant species present a more complex problem. These range from 2·5 to 12·5 mm, mostly 5-10 mm. Only a few, mostly Carpenter Ants, run as large as Termite Type 1 (over 12 mm). Thus the 'middle-sized', 6-12 mm, niche in this material is *exclusively* filled by ants, and only these fall within that category below :

TABLE 11 (cf. Table 7)

SIZE RANGE OF 1530 MEASURABLE INSECTS FROM *Collocalia* FOOD

Month	Species	No. of insects	Percentage of this length-range		
			–5·5 mm (small ants, termites, & all 'others')	6-12 mm (larger ants)	12+ mm (largest ants & larger termites)
November	*salangana*	284	36	54	10
	maxima	132	58	11	31
				42	
February	*salangana*	83	98	2	0
	maxima	108	37	62	1
				63	
March	*salangana*	740	67	9	24
	maxima	183	23	77	0
				77	
		1530			

Thus, although smaller *salangana* regularly has twice as many insects as larger *maxima* (Table 7) and dominates the larger termite sector in proportion to the latter bird's smaller gross intake, twice in three times *maxima* has well over half its food in the middle range ; and when *salangana* dominates here (with the same ant species), *maxima* has stepped up the food size. Therefore—as usual—there is no exclusivity for either

*A thoughtful new study of swifts feeding in Puerto Rico shows a big March-August insect peak, with over 90% of available insects less than 5 mm long, only 1·2% exceeding 10 mm, and severe food supply limitations on two swift populations (Kepler 1972).

species by size. But there is a significant tendency for *maxima* to eat fewer and larger items, especially in the *middle* size range.

We have recalculated these and other figures in other ways, without any fresh insights resulting. In the end it has to be concluded that size alone is not a direct and dominating selective factor except in so far as both species are equally restricted by the nature of their shared feeding processes. Size can, within these limits, be varied according to the overriding consideration of food availability—and chance encounter.

IV. How much do *C. salangana* and *maxima* differ in food habits ?

1. This limited study has been surprisingly unsuccessful in defining any distinct or consistent differentiation or specialization of feeding habits or food for two sympatric *Collocalia* breeding numerously together in Sarawak caves and feeding together in the super-canopy.

2. There is an indistinct *tendency* for larger *maxima* to fly further, stay out longer and go longer on less ; and even more erratically to fly a little higher, though apparently both swiftlets intermix completely at (crucial) ant/termite swarms (cf. 7 below).

3. *C. maxima*, however, seems to 'prefer' more large fat female ants, *salangana* more large termites, small ants and other small insects (Tables 10-11). But there is much bird-to-bird and day-to-day variation and overlap, especially when swarms are scarce. At times either bird 'might take anything manageable that's flying' (Dr Rothschild agreeing with writer).

4. Of 22 families and subfamilies of insect identified in *salangana* stomachs, 8 were not recorded in *maxima* (Tables 2-3) ; but only 1 of these was other than occasional (rare) in the former. Rothschild calculated food common to both birds on three main samples :

Table 12

November	23%
February ..	66%
March ..	6% (fewer *maxima* in sample)

Taking all three lots and refining further from Dr Brown's later ant-analysis, 94% by insect item and about 98% by bulk was of forms found in both birds at least once. All the common foods (ants, termites and two beetle families) were at some stage shared.

5. Looked at another way and momentarily forgetting western ideas applied to the Indian sub-regional equatorial setting, it might even seem stranger that two so-close bird species ate differently in identical context than that both ate everything available (and exclusive to them) they could equitably swallow, especially since there is significant supporting evidence that insect food of *all* kinds may be in highly erratic supply seasonally (Ward 1969 for Singapore ; Fogden 1972 for Sarawak ; cf. Kepler 1972 for Puerto Rican Swifts).

6. Differences might be sought elsewhere. Collection and utilization of nest materials, with associated tactile habits, are suggested as one sector, and will be the subject of a following paper.

7. A residual (difficult) question remains : why does *maxima* often seem to be taking less food, both by numbers and to a lesser extent weight ? The verb ' seem ' is used purposefully. It is possible that this result is methodological. In retrospect, netting more birds coming in full darkness might have been illuminating, though it cannot have changed the overall picture as regards food spectrum. But if, as is quite likely (cf. Appendix), some ants and termites (especially) swarm best after sunset and into full dark, the writer may have too readily followed Medway in accepting that echo-location would not be used for nocturnal swarm-feeding. Alternatively, it could be that *maxima*, with its special nest-salivation and single-egg rhythm may use relatively less energy consumption than *salangana*, which also has a shorter wing ratio ? The question remains open.

APPENDIX : Swarming Insects (cf. II, iii and Tables 5, 8)

The periodicity and distribution of flying ant and termite swarms are evidently crucial for Niah *Collocalia*. The matter has lately been touched upon in another and extensive Sarawak Museum study by Dr Michael Fogden (1972 : 315), apropos general forest bird food, although he only considers termites. As with the wider flying insect problems we are once more faced with very meagre entomological or ecological information. It is agreed that for ants the males swarm first, fly less erratically and are much thinner (by then) than the females which next fly up *slowly*, in prime condition (cf. 7 : 1 sex ratio in III, iii), to copulate. With termites, the swarming is constantly bisexual and copulation occurs *after* falling ; there is no big female preponderance, but both sexes are almost equally fat.

Both Professor Brown (1969-71) at Cornell and Professor l'Abbé G. Van Boven (1972) at Louvain University, Belgium (specializing in tropical Africa) consider that in Borneo's equatorial and climatic conditions, ants and termites of one species or another *might* be swarming on almost any day of the year, subject to weather and other variables. Dr Jean Deligne, University of Brussels, qualifies this view for termites and suggests there may be considerable periods of little or no swarming in Borneo. He has observed this specifically in West Africa (Deligne 1970, 1972), while marked seasonal periodicities have been reported in arid Arizona and equatorially. Single,